New Western North American Taxa of *Arceuthobium* (Viscaceae)

Frank G. Hawksworth
USDA Forest Service, Rocky Mountain Forest and Range Experiment Station,
Fort Collins, Colorado 80526, U.S.A.

Delbert Wiens
Department of Biology, University of Utah, Salt Lake City, Utah 85112, U.S.A.

Daniel L. Nickrent
Department of Plant Biology, Southern Illinois University, Carbondale, Illinois 62901, U.S.A

ABSTRACT. Several new names are proposed for a taxonomic revision of the dwarf mistletoes (*Arceuthobium*). Two new species from northwestern California and southwestern Oregon are described: *A. siskiyouense*, a parasite of knobcone pine, and *A. monticola*, a parasite of western white pine. Also described as new is *A. littorum*, a parasite of Monterey and bishop pines in coastal California. *Arceuthobium tsugense* is segregated into two subspecies: subspecies *tsugense*, primarily parasitic on western hemlock, and subspecies *mertensianae*, primarily parasitic on mountain hemlock.

In preparing a revision of our monograph on dwarf mistletoes (*Arceuthobium*, Viscaceae) (Hawksworth & Wiens, 1972) and for our treatment of the Viscaceae for the new Jepson *Manual of the Flowering Plants of California*, we have continued to investigate the systematics of this economically important genus of conifer parasites (Hawksworth & Wiens, 1976, 1977, 1980, 1984, 1989; Nickrent, 1986, 1987; Nickrent & Butler, 1989, 1990, 1991; Nickrent & Stell, 1990; Nickrent et al., 1984). Here we describe three new species that parasitize pines in Oregon and California, and we also segregate the hemlock dwarf mistletoe into two subspecies. Two of the new species are endemic to the Siskiyou-Klamath Mountains floristic province of northwestern California and southwestern Oregon, an area well known for its high degree of plant endemism (Smith & Sawyer, 1988).

Only brief descriptions of the new taxa, their relationships to closely related taxa, and selected collections representing the host and geographic distribution of the new taxa are cited here. Additional descriptions, illustrations, complete specimen citations, and distribution maps will be presented in our revised monograph of the genus, which is nearing completion. The methods used for our morphological analyses are as described by Hawksworth & Wiens (1972).

Arceuthobium siskiyouense Hawksworth, Wiens & Nickrent, sp. nov. TYPE: U.S.A. Oregon: Josephine County, Oregon Mountain Road, 6 mi. SW of O'Brien, parasitic on *Pinus attenuata*, T. 41 S., R. 9 W., Sect. 9, 42°01′N, 123°46′W, elevation 650 m, 20 July 1987, *D. Wiens 6756* (holotype, US; isotypes, FPF, MO, ORE, OSC, UC).

Plantae 6–10 (8) cm altae; surculi brunnei, parce flabellate ramosi; surculi principales basi 2–2.5 mm diam., internodiis tertiis 6–15 (9) mm longis, 2 mm latis; flores staminati 3–4-meri; fructus maturi 4 mm longi, 2.5 mm lati; anthesis mense Septembri; fructus maturitas mense Septembri–Octobri. In *Pino attenuata* parasiticae.

Plants 6–10 (mean 8) cm tall, brownish, flabellately branched, predominant shoots 2–2.5 mm diam. at base, third internode from base 6–15 (mean 9) mm long and 2 mm wide; staminate flowers 3- or 4-partite; mature fruit 4 mm long and 2.5 mm wide; anthesis in September; fruits mature in September and October; parasitic principally on *Pinus attenuata*.

We previously included this dwarf mistletoe under *A. campylopodum* (Hawksworth & Wiens, 1972, 1984), but noted an anomalous situation near Gasquet, Del Norte County, California, where a dwarf mistletoe (then presumed to be *A. campylopodum*) was common on *Pinus attenuata* but rare on associated *P. ponderosa* (Hawksworth & Wiens, 1972). This situation is now readily explained, because the taxon on *P. attenuata* is *A. siskiyouense*, not *A. campylopodum*.

Arceuthobium siskiyouense is a local endemic restricted to the Siskiyou-Klamath Mountains of southwestern Oregon (Curry and Josephine counties)

TABLE 1. Comparison of some characters of *Arceuthobium siskiyouense* and *A. campylopodum* in the Siskiyou-Klamath Mountains. Means are in parentheses.

Character	*A. siskiyouense* (19 collections)	*A. campylopodum* (17 collections)
Shoot height	6–10 (8) cm	10–14 (12) cm
Basal shoot diameter	2–2.5 mm	3–6 mm
Third internode	6–15 (9) × 2 mm	11–17 (14) × 3–3.5 mm
Mature fruit	4 × 2.5 mm	6 × 3.5 mm
Witches' brooms	None	Well developed
Peak anthesis	September	August
Peak seed dispersal period	September–October	September–October
Elevational range	400–1,200 m	50–2,400 m
Parasitism of *Pinus ponderosa* and *P. jeffreyi*	Rare	Common
Parasitism of *P. attenuata*	Common	Rare

and adjacent northwestern California (Del Norte, Humboldt, and Siskiyou counties). Its known elevational range is from 400 to 1,200 m. In marked contrast, *A. campylopodum* has a wide distribution from northern Idaho and northern Washington to Baja California. The two species are sympatric in several areas but retain their distinctive morphological shoot and fruit characteristics. Their flowering periods partially overlap, but there is no evidence of hybridization between them, thus further supporting their specific status.

Pinus attenuata is the most common host of *A. siskiyouense*. The mistletoe will rarely parasitize *P. ponderosa*, *P. jeffreyi*, and *P. contorta* subsp. *contorta*, but only in areas where these species grow in close association with infected *P. attenuata*. *Arceuthobium siskiyouense* retains its morphological integrity in such "host crossovers," providing further evidence supporting its specific segregation. Furthermore, inoculation tests on *Pinus attenuata* with *A. siskiyouense* (from the Gasquet area) in the central Sierra Nevada foothills at Camino (elevation 900 m) resulted in the exceptionally high infection rate of 86 percent. Inoculations on the same host with *A. campylopodum* seed from *P. jeffreyi* on the Plumas National Forest resulted in only 11 percent infection (R. F. Scharpf, pers. comm.).

Arceuthobium siskiyouense differs from *A. campylopodum* primarily in its shorter, more slender shoots, smaller fruits, later flowering period, absence of witches' broom formation, and varying host relationships (Table 1). Electrophoretic evidence also confirms the distinctness of this taxon (Nickrent & Butler, 1991).

Paratypes: on *Pinus attenuata*, except as noted. U.S.A. CALIFORNIA: Del Norte Co., Gasquet, *Tracy 16464* (CAS, JEPS, UC, VS, WTU); Gordon Mtn., *Newcomb 165* (UC); Bear Wallows, 2 mi. N of Sanger Peak, *Kildare 8785* (CAS); 6 mi. NE of Gasquet on old toll road, on *P. ponderosa*, *Hawksworth & Wiens 867* (FPF) and on *P. contorta* subsp. *contorta*, *Hawksworth & Wiens 866* (FPF); 18 Mile Creek Canyon, Elk Camp Ridge, on *P. contorta* subsp. *contorta*, *Parks & Parks 24063* (UC); 2.5 mi. NW of Black Butte, *Tinnin & Kirkpatrick 1A* (FPF); 2 mi. S of Hazelview Summit on Rte. 199, *Hawksworth 2272* (FPF). Humboldt Co., NW of Scotia, *Miller FP98033* (PFRS). Siskiyou Co., Russian Creek, *Butler 273* (UC); 3 mi. N of Branch Guard Sta., *Kuijt 1277* (UC); 16 mi. N of Happy Camp on O'Brien rd., *Hawksworth & Hinds 1001* (FPF). OREGON: Curry Co., 12 mi. NNW of Agness, *Graham s.n.* (FPF); W side of Vulcan Peak, *Denton 3689* (WTU); SW slope of Iron Mtn., *Baker 3100* (ID). Josephine Co., O'Brien, on *Pinus contorta* subsp. *contorta*, *Weir 3187* (ILL); and on *Pinus jeffreyi*, *Lewis*, 1917 (FPF, ILL); 5 mi. W of Grants Pass, on *P. jeffreyi*, *Graham*, 1964 (FPF); Bain Station on Forest Service road 112, on *P. contorta* subsp. *contorta*, *Mathiasen 8605* (FPF); 2 mi. E of Cave Jct., *Theisen*, 1965 (FPF); near Lookout Gap, 20 air mi. S of Galice, on *P. jeffreyi*, *Graham*, 1965 (FPF); 0.5 mi. S of Galice-Agness road on Hobson Horn road, *Hawksworth 2333* (FPF); Wonder, on *P. jeffreyi*, *Mitchell FP68212* (FPF); Mt. Peavine, near Galice, *Childs FP91615* (OSC).

Arceuthobium monticola Hawksworth, Wiens & Nickrent, sp. nov. TYPE: U.S.A. Oregon: Josephine County, 7 mi. S of O'Brien on Old Gasquet Toll Road (Oregon Mountain Road); parasite on *Pinus monticola*, T. 41 S., R. 9 W., Sect. 9, 42°01′N, 123°46′W, elevation 650 m, 20 July 1987, *D. Wiens 6757* (holotype, US; isotypes, FPF, MO, ORE, OSC, UC).

Plantae 5–10 (7) cm altae; surculi brunnei, parce flabellate ramosi; surculi principales basi 2–4 (3) mm diam., internodiis tertiis 8–15 (12) mm longis, 1.5–2 mm latis; flores staminati 3-meri; fructus maturi 4–4.5 mm longi, 2–2.5 mm lati; anthesis mense Julio–Augusto; fructus maturitas mense Octobri–Novembri. In *Pino monticola* parasiticae.

Plants 5–10 (mean 7) cm tall, brownish, flabellately branched; dominant shoots 2–4 (mean 3) mm

TABLE 2. Comparison of some characters of *Arceuthobium monticola* and *A. californicum*. Means are in parentheses.

Character	*A. monticola* (26 collections)	*A. californicum* (8 collections)
Shoot color	Brownish to reddish	Yellow to greenish
Shoot height	5–10 (7) cm	6–14 (8) cm
Basal shoot diameter	2–4 (3) mm	1.5–4 (2) mm
Third internode	8–15 (12) × 2 mm	5–16 (10) × 1.5 mm
Mature fruit	4 × 2 mm	4 × 2.5 mm
Fruit color	Bluish	Greenish
Peak anthesis	July–August	July
Peak seed dispersal	October–November	September
Parasitism of:		
Pinus monticola	Common	Rare
Pinus lambertiana	Rare	Common

diam. at the base; third internode from the base 8–15 (mean 12) mm long and 1.5–2 mm wide; staminate flowers 3-partite; mature fruit 4–4.5 mm long and 2–2.5 mm wide; anthesis July and August; fruits mature in October and November; parasite principally on *Pinus monticola*.

Previously we included this taxon under *Arceuthobium californicum* (Hawksworth & Wiens, 1972). However, subsequent field and laboratory studies have demonstrated that it is a distinct species endemic to the Siskiyou and Klamath mountains of southwestern Oregon (Coos, Curry, and Josephine counties) and adjacent northwestern California (Del Norte County). Its known elevational range is from 700 to 1,600 m. To our knowledge, it is not sympatric with *A. californicum*, which is apparently confined to California.

Arceuthobium monticola differs from *A. californicum* in its much darker shoot color, later flowering and seed dispersal periods, and occurrence primarily on *Pinus monticola* (Table 2). Electrophoretic evidence also confirms the distinctness of these two taxa (Nickrent & Butler, 1991).

Paratypes: on *Pinus monticola* except as noted. U.S.A. CALIFORNIA: Del Norte Co., 0.5 mi. E of Sourdough Jct., ca. 10 air mi. N of Gasquet, *Miller*, 1969 (FPF); Black Butte, *Theisen & Bynum*, 1968 (FPF), and on *Picea breweriana*, *Mathiasen 8609* (FPF); 2.4 mi. W of Smith River near Lee Brown Crossing, *Mathiasen 8606* (FPF); 0.6 mi. N of Ship Mt. Lookout on Little Jones Creek road, *Mathiasen 8502* (FPF); 0.5 mi. N of Black Butte, *Mathiasen 8607* (FPF); 3.0 mi. E of Smith River bridge, 10 mi. N of Gasquet, *Nickrent & Wiens 2705* (FPF, ILL); Lower Coon Mtn., 1 mi. SW of Camp 6 Lookout, *Mastrogiuseppe & Mastrogiuseppe 153* (WS). OREGON: Coos Co., 13 air mi. S of Powers, *Mathiasen 8610* (FPF). Curry Co., Saddle Mtn., ca. 15 air mi. ESE of Gold Beach, *Bynum*, 1967 (FPF) and on *Picea breweriana*, *Bynum*, 1967 (FPF); 0.2 mi. N of Snow Camp Fire Lookout, *Mathiasen 8601* (FPF), and on *P. jeffreyi*, *Mathiasen 8602* (FPF); 14 mi. ESE of Gold Beach, *Wiens 6793* (FPF); Windy Creek, N of Loeb State Park, *Wiens 6794* (FPF). Josephine Co., Oregon Mt., 14 mi. SW of Cave Jct., on *P. lambertiana*, *Weir 3191* (FPF, ILL).

Arceuthobium littorum Hawksworth, Wiens & Nickrent, sp. nov. TYPE: U.S.A. California: Mendocino County, 3.0 mi. E of Noyo on State Highway 20, on *Pinus muricata*, elevation 30 m, 12 Dec. 1989, *R. L. Mathiasen 8940* (holotype, US; isotypes, CAS, FPF, HSC, MO, UC).

Plantae 10–20 (12) cm altae; surculi brunneo-virides, parce flabellate ramosi; surculi basi 2–5 (3.5) mm diam., internodiis tertiis 10–20 (15) mm longis, 2–5 (3.5) mm latis, flores staminati 4-meri; fructus maturi 3–5 mm longi; anthesis mense Augusto–Septembri; fructus maturitas mense Septembri–Octobri. In *Pino radiata* et *Pino muricata* parasiticae.

Plants 10–12 (mean 12) cm tall; brown to green, flabellately branched; dominant shoots 2–5 (mean 3.5) mm diam. at base; third internode 10–20 (mean 15) mm long and 2–5 (mean 3.5) mm wide; staminate flowers 4-partite, mature fruit 3–5 mm long; anthesis August and September; fruits mature in September and October; parasite principally on *Pinus radiata* and *P. muricata*.

Previously this taxon was included in *Arceuthobium occidentale* Engelm. (Hawksworth & Wiens, 1972, 1984). We now separate *A. littorum* as a distinct species parasitic on *Pinus radiata* D. Don, *P. muricata* D. Don, and rarely *P. contorta* Dougl. ex Loud. subsp. *bolanderi* (Parl.) Critch. It occurs from Fort Bragg (Mendocino County) to Cambria (San Luis Obispo County) and ranges in elevation from near sea level to about 250 m.

Arceuthobium littorum differs from *A. occiden-*

TABLE 3. Comparison of some characters of *Arceuthoblium littorum* and *A. occidentale*. Means are in parentheses.

Character	*A. littorum* (8 collections)	*A. occidentale* (9 collections)
Shoot height	10–20 (12) cm	6–12 (8) cm
Mean shoot diameter	2–5 (3.5) mm	1.5–4 (2.3) mm
Third internode	15 × 3.5 mm	12 × 2 mm
Shoot color	Dark brown to olive green	Light green to straw
Mature fruit length	4–5 mm	3.5–4.5 mm
Staminate flowers	4-partite	3- or 4-partite
Shoot habit	In dense globose clusters	Open, scattered shoots
Witches' brooms	Large, nonsystemic	Usually none
Peak anthesis	August–September (24 observations)	October–November (176 observations)
Peak seed dispersal	September–October (31 observations)	October–December (187 observations)
Mean fruit maturation	14 months	13 months
Elevational range	Near sea level to 250 m	100–1,200 m

tale in several features. *Arceuthobium occidentale* is primarily a parasite of *Pinus sabiniana* in the foothills surrounding the Central Valley of California. It is not sympatric with *A. littorum*, which is confined to a narrow band within about 5 km of the sea. Verticillate branching of *A. littorum* is somewhat more common than for *A. occidentale* (Mark & Hawksworth, 1981). Electrophoretic studies confirm that *A. littorum* is the most distinct member of the *A. campylopodum–A. occidentale* complex (Nickrent & Butler, 1990). Additional differences between *A. littorum* and *A. occidentale* are given in Table 3.

Pleistocene fossils of *A. littorum* (originally reported as *A. campylopodum*) were found associated with *P. muricata* and *P. radiata* in Marin County (Tomales Bay) and Santa Barbara County (Carpinteria and Santa Cruz Island) (Chaney & Mason, 1933). These 30,000–40,000-year-old populations are characterized by mostly 4-partite staminate flowers, a characteristic of modern *A. littorum*. This dwarf mistletoe is still extant near Tomales Bay, but is extinct at the other two localities.

Paratypes. U.S.A. CALIFORNIA: Alameda Co., Berkeley, on planted *P. radiata, Offord & Scharpf*, 1964 (FPF). Marin Co., Inverness Ridge, on *P. muricata, Howell 19686* (CAS, UC). Mendocino Co., Fort Bragg, on *P. muricata, Mason 5639* (UC); mouth of Gualala River, on *P. muricata, Bacigalupi 1808* (CAS); Van Damme State Park, on *P. muricata, Kuijt 1214* (UC); 2.9 mi. E of Point Arena, on *P. muricata, Nickrent 2719* (FPF, ILL); 2.7 mi. SE of Fort Bragg, on *P. contorta* subsp. *bolanderi, Nickrent 2716* (FPF, ILL); Van Damme State Park, on *P. contorta* subsp. *bolanderi, Kuijt 1215* (UC); just E of airport near Albion, on *P. contorta* subsp. *bolanderi, Peterson 65-116* (FPF); White Sands near Mendocino City, on *P. muricata, Eastwood 18836* (CAS); 2 mi. S of Anchor Cove, on *P. muricata, Wolf 1342* (CAS). Monterey Co., Pebble Beach, Carmel, on *P. radiata, Boyce 33* (FPF); Carmel, on *P. radiata, von Schrenk*, 1920 (MO); Carmel Highlands above Yankee Point, on *P. radiata, Balls 23608* (WTU); Point Lobos State Park, on *P. radiata, Lee & Mason 9153* (UC); Gibson Creek, on *P. radiata, Wheeler 4452* (POM); Monterey, on *P. radiata, Parry*, 1850 (MO); Pacific Grove, on *P. radiata, Davy 7064* (UC); Cypress Point, on *P. radiata, Abrams 7660* (RM, US); Huckleberry Hill, Carmel, on *P. muricata, Mason 5515* (UC). San Luis Obispo Co., Cambria, on *P. radiata, Gill FP68079* (FPF); between Cambria and Cambria Pines on Roberts road, on *P. radiata, Hawksworth 2264* (FPF). Sonoma Co., Fort Ross, on *P. muricata, Mason 4285* (UC); Kruse Rhododendron State Park on Rte. 1, on *P. muricata, Nickrent 2722* (FPF, ILL).

Arceuthobium tsugense (Rosendahl) G. N. Jones, Univ. Wash. Publ. Biol. 5: 139, 1936.

In our monograph (Hawksworth & Wiens, 1972), we commented on the unusually broad host range of *A. tsugense*, which not only encompassed both western species of *Tsuga*, but also several species of *Abies*, *Picea*, and *Pinus*. The occurrence of a form or "pathotype" (Hunt & Smith, 1978) on shore pine in British Columbia and the San Juan Islands of Washington had long been known (Hawksworth & Wiens, 1972; Hunt & Smith, 1978; Smith, 1971, 1974; Smith & Wass, 1976, 1979; Wass, 1976; Kuijt, 1956), although its taxonomic status has not been previously established. Field and laboratory studies of *A. tsugense* now show that this species is comprised of at least three segregates (Hawksworth, 1987; Mathiasen & Hawksworth, 1988).

The populations on mountain hemlock (subsp. *mertensianae*) and western hemlock (subsp. *tsugense*) are described here as subspecies because of

TABLE 4. Comparison of the shoot height of the two subspecies of *Arceuthobium tsugense*.

Subspecies	Number of collections	Shoot height	
		Range	Mean and standard error
subsp. *tsugense* (western hemlock race)	86	3–13 cm	6.9 ± 0.2 cm
subsp. *mertensianae*	58	3–9 cm	5.3 ± 0.2 cm

their distinct host ranges, shoot sizes, and marked isozyme differences (Nickrent, 1988; Nickrent & Stell, 1990). The populations of subspecies *tsugense* on western hemlock and shore pine are considered to be host races because they are morphologically and phenologically similar. Also, the isozyme patterns of the two races are similar, and they are sympatric in many stands (Nickrent & Stell, 1990).

Arceuthobium tsugense (Rosendahl) G. N. Jones subsp. **tsugense,** Univ. Wash. Publ. Biol. 5: 139, 1936.

As presently interpreted, this subspecies consists of two host races, one primarily on *Tsuga heterophylla* and one on *Pinus contorta* subsp. *contorta*. An intensive series of field and inoculation studies in British Columbia (Smith, 1971, 1974; Smith & Wass, 1976, 1979; Wass, 1976) showed that the two races are similar morphologically but differ in their host relationships. In inoculation tests, the *T. heterophylla* race produced very low infection levels on *P. contorta* subsp. *contorta*, but the few infections produced developed abundant aerial shoots. In contrast, the *P. contorta* subsp. *contorta* race produced a moderate infection level on *T. heterophylla*, but only a few of these produced aerial shoots (Smith & Wass, 1979). Maximum shoot height of the *T. heterophylla* race was about 30 percent taller than shoots of the *P. contorta* subsp. *contorta* race (Smith, 1971). Results from inoculation trials in two areas in British Columbia confirm the morphological similarity of the two races (E. Wass, pers. comm.). The only statistically significant difference between the populations in the two areas was that the fruits of the *P. contorta* subsp. *contorta* race were slightly longer and wider than those of the *T. heterophylla* race. Also, the peaks in anthesis and seed dispersal occurred about 10 days earlier in the *P. contorta* subsp. *contorta* race than in the *T. heterophylla* race in the same areas.

See Hawksworth & Wiens (1972) for information on the distribution of the two races. In general:

1. The western hemlock race is distributed from southeast Alaska (from near Haines, at nearly 60°N) throughout the coastal western hemlock forests of British Columbia, Washington, and Oregon to Humboldt and Del Norte counties in northwestern California (Hawksworth, 1987; Hawksworth & Wiens, 1972; Wood, 1986). Its principal host is *Tsuga heterophylla*. *Abies amabilis* and *A. procera* are frequently parasitized, but usually only where these trees are associated with infected *T. heterophylla*. This race is rare on associated *Tsuga mertensiana* and *Pinus monticola*. Inoculation tests have shown that several other trees from outside the natural range of western hemlock race are susceptible (Smith, 1965, 1970a, b, 1972, 1974; Smith & Craig, 1968; Smith & Wass, 1979; Weir, 1918). The western hemlock race is distributed from elevations near sea level in Alaska, British Columbia, Washington, Oregon, and California to about 1,200 m in southern Oregon.

2. The shore pine race is local in southern British Columbia (on the east shore of Vancouver Island and along the adjacent mainland coast) and on Orcas Island, Washington (Hawksworth, 1987; Smith & Wass, 1976; Wass, 1976). The northern limits of the race are poorly known. Two additional collections of a dwarf mistletoe on shore pine more than 450 km north of the main range of the shore pine race have been reported: at Port Clements on the Queen Charlotte Islands and at Terrace on the mainland (Wass, 1976). Studies of these populations are needed to determine whether they are indeed the shore pine race or merely rare crossovers of the western hemlock race. The principal host of the shore pine race is *Pinus contorta* subsp. *contorta*. It is usually rare on associated *Tsuga heterophylla*, but in some areas on Vancouver Island both trees are infected in mixed stands. Possibly these cases represent mixed populations of the two races. The shore pine race occasionally parasitizes associated *Pinus monticola* (Kuijt, 1956). Inoculation tests have shown that several other tree species from outside the natural range of the shore pine race are susceptible (Smith, 1970a, b, 1974; Smith & Craig, 1968; Smith & Wass, 1979). The shore pine race is distributed from about 100 to 800 m.

TABLE 5. Differential parasitism of selected hosts of the three segregates of *Arceuthobium tsugense*.

Taxon	*Tsuga heterophylla*	*Tsuga mertensiana*	*Pinus contorta* subsp. *contorta*	*Pinus monticola*
subsp. *tsugense*				
western hemlock race	Common	Very rare	Rare	Rare
shore pine race	Rare	*	Common	Rare
subsp. *mertensianae*	Immune	Common	*	Common

* Tree does not occur naturally within the range of the dwarf mistletoe.

Arceuthobium tsugense (Rosendahl) G. N. Jones subsp. **mertensianae** Hawksworth & Nickrent, subsp. nov. TYPE: U.S.A. Oregon: Douglas County, 16 mi. N of Union Creek on State Highway 230, on *Tsuga mertensiana*, elevation ca. 1,500 m, 2 Jan. 1990, *R. L. Mathiasen 9002* (holotype, US; isotypes, FPF, MO, ORE, OSC, UC, UWT).

Plantae 3–9 (5) cm altae; anthesis mense Augusto–Septembri; fructus maturitas mensis Septembri–Octobri. In *Tsugo mertensiana* parasiticae.

Plants similar to subspecies *tsugense* but are 3–9 (mean 5) cm tall; anthesis in August and September; fruits mature in September and October; parasite principally on *Tsuga mertensiana*.

The two subspecies are generally similar morphologically, but in subspecies *mertensianae* the shoots average about 30 percent shorter than in the western hemlock race of subspecies *tsugense* (Table 4). The differences are statistically highly significant ($t = 47.08$, $P = .0001$). We do not have sufficient material to make a comparable morphological analysis of the shore pine race of *A. tsugense*.

The phenology of flowering of the two subspecies is similar except that anthesis averages about 1 week earlier in the western hemlock race of subspecies *tsugense* (peak anthesis in August, with extremes from late July to late September, 56 observations) than for subspecies *mertensianae* (peak anthesis from mid-August to mid-September, 33 observations). The phenology data are based on observations throughout the range of the two taxa. In contrast to flowering, the seed dispersal period for subspecies *tsugense* (late September to early November, 57 observations) averages about 2 weeks *later* than for subspecies *mertensianae* (early September to late October, 31 observations), thus the fruit maturation period averages about 13 months in subspecies *tsugense* and 14 months for subspecies *mertensianae*.

Perhaps the marked differences in susceptibility of the two hemlocks to the two subspecies of the parasite is explained by the wide taxonomic differences of the two trees. For example, Page (1988) indicated that mountain hemlock is such a distinct entity that it should be segregated from *Tsuga* as a monotypic genus, *Hesperopeuce* Lemmon. If this classification is accepted, the scientific name for mountain hemlock becomes *Hesperopeuce mertensiana* (Bong.) Rydb. The two genera are said to differ in needle anatomy and morphology, shoot and cone morphology, bark features, and pollen morphology (Page, 1988). In another study, Farjon (1988) named the southern populations of *Tsuga mertensiana* as subspecies *grandicona* (the cones being 4–8 cm long, compared to 2–5 cm long for cones of the typical subspecies, *mertensiana*). All populations of *Tsuga mertensiana* from California and Nevada are referable to subspecies *grandicona*. The northern limits of this subspecies are not clear, but it ostensibly occurs as far north as the Siskiyou Mountains near the California–Oregon border. Thus, both subspecies are parasitized by *A. tsugense* subsp. *mertensianae*, but the mistletoe is much more common within the range of subspecies *grandicona*. In any case, the strong taxonomic differences between the two species of hemlock may help explain the unique host relations of the two subspecies of *A. tsugense*.

The three segregates of *A. tsugense* are most easily distinguished by their differential parasitism of *Tsuga heterophylla*, *Tsuga mertensiana*, *Pinus contorta* subsp. *contorta*, and *Pinus monticola* (Table 5). Further information on the host relationships of these mistletoes will be given in our revised monograph.

Arceuthobium tsugense subsp. *mertensianae* ranges from extreme southern British Columbia to the central Sierra Nevada in California, but it is most common from central Oregon southward. Its elevational range is from about 800 m in British Columbia to 2,500 m in central California. The northern limits of subspecies *mertensianae* have not been determined, but it occurs at least as far north as the Cypress Bowl area just north of Vancouver, British Columbia (Van Sickle & Fiddick, 1982). It is common at the Mt. Baker Ski Area in northern Washington. There are a number of collections, of

what is presumably this dwarf mistletoe, on the east side of the Cascade Mountains in Chelan County, Washington, but the distribution of the taxon there is poorly documented.

Arceuthobium tsugense subsp. *tsugense* rarely parasitizes *Tsuga mertensiana* in areas of Alaska where this tree is associated with infected *Tsuga heterophylla* (Shaw, 1982) and perhaps elsewhere.

The principal host of *A. tsugense* subsp. *mertensianae* is *Tsuga mertensiana*, and we have not found it parasitizing *Tsuga heterophylla*, even where this tree is closely associated with infected *T. mertensiana*. The mistletoe also parasitizes *Pinus monticola*, *P. albicaulis*, *Abies procera*, *A. amabilis*, and *A. lasiocarpa*, but usually only in areas where these trees are closely associated with infected *Tsuga mertensiana*.

Additional specimens examined: on *Tsuga mertensiana*, except as noted. U.S.A. CALIFORNIA: Alpine Co., Mosquito Lake, 11 mi. NE of Alpine, *Hawksworth & Scharpf 665* (FPF), and on *Pinus monticola*, *Hawksworth & Scharpf 666* (FPF). Placer Co., Emigrant Gap, *Jones*, 1881 (POM). Plumas Co., Mt. Elwell, *Lieberg 5363* (ILL, US); 0.4 mi. NE of Hawlsey Lake, *Mathiasen 8513* (FPF). Shasta Co., Lassen National Park, 2.5 mi. N of S entrance, *Wiens 3235* (COLO, FPF); 0.7 mi. E of Kings Creek Ground on Rte. 89, *Mathiasen 8511* (FPF). Sierra Co., Hawlsey Lake, 3 mi. W of Gold Lake, on *Pinus monticola*, *Mathiasen 8514* (FPF). Siskiyou Co., Marble Mtns., Kidder Creek, *Gill & Sargent FP68180* (FPF); Chimney Rock Lake, *Hemphill*, 1968 (FPF, UT) and on *Picea breweriana*, *Hemphill*, 1968 (FPF, UT); near Chimney Rock, on *Pinus monticola*, *Hemphill*, 1968 (FPF, UT); Little Marble Valley, *Mathiasen 8623* (FPF); Siskiyou Mtns., Applegate Creek Divide, *Meinecke FP97938* (PFRS) and on *Picea breweriana*, *Meinecke FP97941* (PFRS); N Slope of White Mtn., *Mathiasen 8629* (FPF), and on *P. monticola*, *Mathiasen 8628* (FPF); Trinity Alps, Snowslide Lake, *Mathiasen 9016* (FPF). Tehama Co., Mineral, *Lory FP97940* (PFRS). Trinity Co., 1–2 mi. S of Helen Lake, *Scharpf FP38027* (PFRS). OREGON: Clackamas Co., near Frog Lake, Wapinita Pass, *Mathiasen 8643* (FPF). Coos Co., Iron Mtn., *Baker*, 1946 (ID, OSC); 10 air mi. NNE of Agness, *Graham*, 1965 (FPF). Curry Co., Snow Camp Mtn., on *Pinus monticola*, *Nickrent & Wiens 2701* (FPF, ILL). Deschutes Co., 11 mi. W of Sisters on McKenzie Pass road, *Hawksworth & Hinds 991* (FPF), and on *Abies lasiocarpa*, *Hawksworth & Hinds 992* (FPF); 1 mi. W of Elk Lake near trail to Horse Lake, *Mathiasen 8645* (FPF). Douglas Co., just N of Crater Lake National Park on Diamond Lake road, *Graham*, 1964 (FPF); E side of Diamond Lake, 1 mi. N of jct. of Rtes. 230 & 138 on 138, *Mathiasen 8616* (FPF); 4 mi. SW of Windigo Pass on Lemolo Lake road, *Hawksworth 2339* (FPF), and on *Pinus monticola*, *Hawksworth 2340* (FPF). Jackson Co., Union Creek, *Applegate 6038* (CAS); Huckleberry Mtn., 10 mi. NE of Prospect, *Graham*, 1965 (FPF). Klamath Co., Crater Lake National Park, Annie Springs, *Gill FP68184* (FPF); Wineglass, on *Pinus albicaulis*, *Gill FP68182* (FPF); 5 mi. E of main road on N rim of Crater Lake, *Hawksworth & Wiens 624* (FPF), and on *Pinus albicaulis*, *Hawksworth & Wiens 625* (FPF); 2 mi. N of Windigo Pass, *Hawksworth & Wiens 621* (FPF) and on *Pinus monticola*, *Hawksworth & Wiens 622* (FPF); 8 air mi. N of Lake of the Woods on Cold Springs road, *Hawksworth 2375* (FPF). Lane Co., McKenzie Pass, on *Pinus albicaulis*, *Gill FP68188* (FPF). Linn Co., Minto Mtn., *Mielke FP40694* (OSC); Marion Lake, *Coville & Applegate 1156* (US); Wildcat Mtn., *Hawksworth 2358* (FPF), on *Abies amabilis*, *Hawksworth 2355* (FPF), and on *Abies procera*, *Hawksworth 2356* (FPF); H. J. Andrews Experimental Forest, near Frissell Point, *Hawksworth 2359* (FPF), on *Abies amabilis*, *Hawksworth 2360* (FPF), and on *Abies procera*, *Hawksworth 2361* (FPF). WASHINGTON: Whatcom Co., Mt. Baker Ski Area, *Mathiasen 9005* (FPF), and on *Abies amabilis*, *Mathiasen 9006* (FPF); Twin Sister Range, *Meunschler 10431* (CAS). Chelan Co., Lyman Glacier W of Lucerne, *Weir 2456* (ILL). Pierce Co., Upper Nisqually Valley, *Allen 303* (CAS, MO, UT). CANADA. BRITISH COLUMBIA: Cypress Bowl Park, Hollyburn rd., *Wood*, 1982 (DAVFP); Lost Lake, Brothers Creek, adjacent to Cypress Bowl Park, *Alexander*, 1972 (DAVFP).

Acknowledgments. We thank Robert L. Mathiasen for making the type collections for two of the new taxa and Richard B. Smith, Robert F. Scharpf, Robert O. Tinnin, Robert L. Mathiasen, Donald M. Knutson, and Ed Wass for information and manuscript reviews. We also thank Job Kuijt for criticisms of an earlier draft of the manuscript and John Hough for assistance with the Latin descriptions.

Literature Cited

Chaney, R. W. & H. L. Mason. 1933. A Pleistocene flora from the asphalt deposits of Carpenteria, California. Publ. Carnegie Inst. Wash. 415: 45–79.

Farjon, A. 1988. Taxonomic notes on Pinaceae I. Proc. Kon. Ned. Akad. Wetensch., Ser. C, Biol. Med. Sci. 91: 31–42.

Hawksworth, F. G. 1987. Taxonomy of hemlock dwarf mistletoe. Pp. 45–46 *in* Proc. 34th Western International Forest Disease Work Conference.

——— & D. Wiens. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). Agric. Handb. 401, USDA Forest Service, Washington, D.C.

——— & ———. 1976. *Arceuthobium oxycedri* and its segregates *A. juniperi-procerae* and *A. azoricum* (Viscaceae). Kew Bull. 31: 71–80.

——— & ———. 1977. *Arceuthobium* (Viscaceae) in Mexico and Guatemala: additions and range extensions. Brittonia 29: 411–418.

——— & ———. 1980. A new species of *Arceuthobium* from Central Mexico. Brittonia 32: 348–352.

——— & ———. 1984. Biology and classification of *Arceuthobium*: an update. Pp. 2–17 *in* Gen. Techn. Rep. RM-111, Biology of Dwarf Mistletoes, Proc. of the Symposium, USDA Forest Serv., Fort Collins, Colorado.

——— & ———. 1989. Two new species, nomenclatural changes, and range extensions in Mexican *Arceuthobium* (Viscaceae). Phytologia 66: 5–11.

Hunt, R. S. & R. B. Smith. 1978. Natural infection of two new hosts by hemlock dwarf mistletoe in British Columbia. Canada Plant Dis. Surv. 58(2): 31–32.

Kuijt, J. 1956. A new record of dwarf mistletoe on lodgepole pine and western white pine. Madroño 13: 170–172.

Mark, W. R. & F. G. Hawksworth. 1981. Taxonomic implications of branching patterns in the dwarf mistletoes (*Arceuthobium*). Phytologia 48: 441–444.

Mathiasen, R. L. & F. G. Hawksworth. 1988. Dwarf mistletoes on western white pine and whitebark pine in northern California and southern Oregon. Forest Sci. 34: 429–440.

Nickrent, D. L. 1986. Genetic polymorphism in the morphologically reduced dwarf mistletoes (*Arceuthobium*, Viscaceae). Amer. J. Bot. 73: 1492–1502.

———. 1987. Systematics and population biology of two sibling species of *Arceuthobium* (dwarf mistletoes, Viscaceae). Pp. 597–611 *in* H. Chr. Weber & W. Forstreuter (editors), Proc. IV International Symposium Parasitic Flowering Plants, Marburg, West Germany.

———. 1988. Electrophoretic characterization of host races in hemlock dwarf mistletoe (*Arceuthobium tsugense*). Amer. J. Bot. 75(6), Part 2: 196. [Abstract.]

——— & T. L. Butler. 1989. Electrophoretic evidence supports the recognition of a new species of *Arceuthobium* (Viscaceae) from coastal California. Amer. J. Bot. 76(6): 261–262 (supplement). [Abstract.]

——— & ———. 1990. Allozymic relationships of *Arceuthobium campylopodum* and allies in California. Biochem. Systematics and Ecol. 18: 253–265.

——— & ———. 1991. Genetic relationships in *Arceuthobium monticola* and *A. siskiyouense* (Viscaceae): new dwarf mistletoes from California and Oregon. Biochem. Systematics and Ecol. 19: 305–313.

——— & A. Stell. 1990. Electrophoretic evidence for genetic differentiation in two host races of hemlock dwarf mistletoe (*Arceuthobium tsugense*, Viscaceae). Biochem. Systematics and Ecol. 18: 267–280.

———, S. I. Guttman & W. H. Eshbaugh. 1984. Biosystematics and evolutionary relationships among selected taxa of *Arceuthobium*. Pp. 20–35 *in* Gen. Techn. Rep. RM-111, Biology of Dwarf Mistletoes, Proc. of the Symposium. USDA Forest Serv., Fort Collins, Colorado.

Page, C. N. 1988. New and maintained genera in the conifer families Podocarpaceae and Pinaceae. Notes Roy. Bot. Gard. Edinburgh 45: 377–395.

Shaw, C. G., III. 1982. Mountain hemlock is occasional host for hemlock dwarf mistletoe in Alaska. Plant Dis. 66: 852–854.

Smith, J. P., Jr. & J. O. Sawyer, Jr. 1988. Endemic plants of northwestern California and southwestern Oregon. Madroño 35: 54–69.

Smith, R. B. 1965. Some results of artificial inoculation with western hemlock dwarf mistletoe seed. Canad. Dept. Forest., Bi-Monthly Progr. Rep. 21(6): 3–4.

———. 1970a. Infection of western larch by hemlock dwarf mistletoe. Canad. Dept. Fish. Forest., Bi-Monthly Res. Notes 26: 16–17.

———. 1970b. Infection of Engelmann spruce by hemlock dwarf mistletoe. Canad. Dept. Fish. Forest., Bi-Monthly Res. Notes 26: 14.

———. 1971. Development of dwarf mistletoe (*Arceuthobium*) infections on western hemlock, shore pine and western larch. Canad. J. Forest. Res. 1: 35–42.

———. 1972. Relative susceptibility of coastal and interior western hemlock to hemlock dwarf mistletoe (*Arceuthobium tsugense*). Canad. Dept. Environ., Forest. Serv., Bi-Monthly Res. Notes 28: 17–18.

———. 1974. Infection and development of dwarf mistletoe on plantation-grown trees in British Columbia. Canad. Forest. Serv., Pacific Forest Res. Centre Rep. BC-X-97.

——— & H. M. Craig. 1968. Infection of Scots, Monterey and ponderosa pines by western hemlock dwarf mistletoe. Canad. Dept. Forest. Rural Development, Bi-Monthly Res. Notes 24: 10–11.

——— & E. F. Wass. 1976. Field evaluation of ecological differentiation of dwarf mistletoe on shore pine and western hemlock. Canad. J. Forest Res. 6: 225–228.

——— & ———. 1979. Infection trials with three dwarf mistletoe species within and beyond their known ranges in British Columbia. Canad. J. Pl. Pathol. 1: 47–57.

Van Sickle, G. A. & R. L. Fiddick. 1982. Pacific Region. Pp. 71–79 *in* Canad. Forest. Serv., Forest Insect and Dis. Surv. Annual Rep. 1979.

Wass, E. F. 1976. Ecological study of shore pine stands infested with dwarf mistletoe on southeastern Vancouver Island. Canad. Forest. Serv., Pacific Forest Res. Centre Rep. BC-X-142.

Weir, J. R. 1918. Experimental investigations on the genus *Razoumofskya*. Bot. Gaz. (Crawfordsville) 56: 1–31.

Wood, C. 1986. Distribution maps of common tree diseases in British Columbia. Canad. Forest. Serv., Pacific Forest Centre Inform. Rep. BC-X-281.